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An integrated approach shows different use of water resources from Mediterranean maquis species in a coastal dune ecosystem

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Abstract. An integrated approach has been used to analyse the dependence of three Mediterranean species, *A. unedo* L., *Q. ilex* L., and *P. latifolia* L. co-occurring in a coastal dune ecosystem on two different water resources: groundwater and rainfed upper soil layers. The approach included leaf level gas exchanges, sap flow measurements and structural adaptations between 15 May and 31 July 2007. During this period it was possible to capture different species-specific response patterns to an environment characterized by a sandy soil, with a low water retention capacity, and the presence of a water table. The latter did not completely prevent the development of a drought response and, combined with previous studies in the same area, response differences between species have been partially attributed to different root distributions. Sap flow of *A. unedo* decreased rapidly with the decline of soil water content, while that of *Q. ilex* decreased only moderately. Midday leaf water potential of *P. latifolia* and *A. unedo* ranged between −2.2 and −2.7 MPa throughout the measuring period, while in *Q. ilex* it decreased down to −3.4 MPa at the end of the season. *A. unedo* was the only species that responded to drought with a decrease of its leaf area to sapwood area ratio from 23.9±1.2 (May) to 15.2±1.5 (July). While *A. unedo* also underwent an almost stepwise loss on hydraulic conductivity, such a loss did not occur for *Q. ilex*, whereas *P. latifolia* was able to slightly increase its hydraulic conducitivity. These differences show how different plant compartments coordinate differently between species in their responses to drought. The different responses appear to be mediated by different root distributions of the species and their relative resistances to drought are likely to depend on the duration of the periods in which water remains extractable in the upper soil layers.

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1 Introduction

Coastal ecosystems will be exposed to increasing risks over coming decades due to climate change, sea-level rise, coastal erosion (Nicholls et al., 2007), and a possible increase in atmospheric pollutants. These additional stressors will exacerbate the typical limiting environment of coastal dunes characterized by low nutrient availability, scarce soil water retention potential, soil salinity and sea aerosols (Alley et al., 2003). In Mediterranean climates summer drought represents an additional stress with which the the dune vegetation must cope, but this stress can be partially avoided by deep rooting species when a relatively shallow fresh water table is present (Alessio et al., 2004). However, Regional Circulation Models predict a decrease in precipitations for the Mediterranean Basin (IPCC, 2007), with a consequent increase in depth of the water table. Moreover, coastal ecosystems are often located in the proximity of anthropogenic pollution sources, and the interaction between maquis vegetation and atmospheric pollutants, particularly photochemical oxidants, is complex and not yet fully understood (Ferretti et al., 2007).

As found by Alessio et al. (2004) woody species growing in a coastal dune ecosystem have access to both rainwater and groundwater and differ in the proportions of water used from these two sources. These differences cause difficulties in determining the water use strategy of a given species, i.e. whether the species shows an isohydric or an anisohydric behaviour. Isohydric plants are recognizable from their fairly constant leaf water potential, Ψ_l, independent from the soil water potential Ψ_s, while the Ψ_l of anisohydric plants varies according to the Ψ_s (Tardieu and Simonneau, 1998; Franks et al., 2007). Because of this difference, isohydric plants transpire less water than anisohydric plants as the Soil Water Content (SWC) decreases, a behaviour that is reflected by the nomenclature of "water savers" and "water

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spenders" (Schultz, 2003). However, there is no clear picture of the environmental or evolutionary significance of isohydry or anisohydry, and yet no clear mechanism has been described for either behaviour (Franks et al., 2007). In practice, it is difficult to classify the strategy of a species, as the same species may be considered isohydric during mild droughts and anisoyhdric during strong droughts (Tognetti et al., 2009). Moreover, if part of the root system tapers the water table, midday water potential (Ψ_{MD}, MPa) and predawn water potential (Ψ_{PD}, MPa) may remain unaltered during the summer even if the soil water content decreases in the upper layer of the soil. However, this condition will not necessarily preserve transpiration rates from decreasing as the upper soil layers dries.

In the presence of two different water resources and of a general heterogeneity of the environmental and biotic characteristics of this environment, it is recommended to analyse drought response mechanisms with an integrated approach, combining leaf level and whole plant level studies, including important structural parameters as the ratio between the Leaf Area and the Sapwood Area (LA/SA). Keeping in mind the mass balance between the liquid water phase and the vapour phase, assuming no capacitance, and introducing the analogy with Ohm's law for the hydraulic circuits, we can write:

$$(\Psi_l - \Psi_s) \times K_p = \mathrm{VPD} \times \mathrm{LA} \times g_s \quad (1)$$

where Ψ_l and Ψ_s are the leaf and the soil water potentials, respectively, K_p is the whole plant hydraulic conductance, LA is the whole plant leaf area, g_s is the stomatal conductance per unit leaf area and VPD is the Vapour Pressure Deficit in air. Given the analogy with an electric circuit, the left-hand side of the equation is equal to the sap flow, while the right-hand side corresponds to plant transpiration. After Mencuccini (2003), by adding a term to take hydrostatic pressure into account Eq. (1) can be rearranged in:

$$\Psi_l = \Psi_s - \frac{\mathrm{LA} \times g_s \times \mathrm{VPD}}{K_p} - \rho_w \times g \times h \quad (2)$$

where ρ_w is the density of water, g is the gravity acceleration constant and h is the height. This equation allows to identify the parameters which are sensitive to a change of environmental or physiological conditions. The LA/SA, as well as the leaf area itself, is generally lower in arid regions than in more mesic ones (de Lillis, 1991; Mencuccini and Grace, 1995). Plants may control their water consumption through stomatal activity, changes in LA/SA (Bucci et al., 2004), in xylem vessel dimensions, in root surface or through a combination of these factors. The ability of a species to use different combinations of these factors may depend on its water use strategy: with isohydric species maintaining their leaf area unaltered and anisohydric species been more prone to leaf shedding (Maseda and Fernadez, 2006). In addition, plant response to water drought not only involves different levels (tissue, organ, individual), but the physiological, anatomical or morphological adjustment depends on time scale and apparently tend to increase the overall plant water resistance to flow in the short term and to decrease it in the long term (Maseda and Fernandez, 2006). Perhaps, all compartments of the plant system can compensate for one another in order to tend towards homeostasis, but the ability to predict the physiological activity of a plant from its hydraulic architecture or vice versa is still lacking (Gartner, 1995). It is hence important, in plant-water relation studies, to simultaneously take into account both leaf and whole plant level responses as well as eventual structural changes.

In this paper, we focussed on drought responses of *Arbutus unedo* L., *Quercus ilex* L. and *Phyllirea latifolia* L., three evergreen sclerophyllous species co-occurring in the Mediterranean dune vegetation. Previous studies have dealed with the ecophysiology of these species (e.g. Tretiach, 1993; Peñuelas et al., 1998; Manes et al., 1997a, 2006; Asensio et al., 2007), with *A. unedo* being described as the least drought tolerant (Ogaya et al., 2003), *Q. ilex* showing an intermediate degree of drought adaptations (Filella et al., 1998), and *P. latifolia* being the most resistant to severe drought conditions (Peñuelas et al., 2000; Gratani and Varone, 2004). However, the very few works (Martínez-Vilalta et al., 2002, 2003; Tognetti et al., 2000a) that focussed on the water relations of these three species through an integrated approach do not completely confirm this ranking. Additionally, integrated studies are completely lacking in coastal environments, where plants may respond to site-specific environmental conditions. For example, Castillo et al. (2002) suggested a relationship between root distribution and leaf water potential development during drought in three species growing over a Mediterranean dune system. While Alessio et al. (2004) showed that species growing over a coastal dune system strongly depend on reliable deep water resources during the drought period, and that this dependence differs among species. Important from the study of Alessio et al. (2004) is the ability of *A. unedo* to switch actively between shallow and deep soil water resources. Our integrated study at different levels in the soil-plant-atmosphere continuum may help to better understand the response of woody plants to changing environmental conditions in such a complex ecosystem as the coastal sand dunes. The hypothesis to be tested is that, among the three species, *A. unedo* is the one which responds more markedly to the drying of the upper soil layers because of its higher dependence on a dual water resource use.

2 Material and methods

2.1 Site description and vegetation characteristics

The study site is located inside the Presidential Estate of Castelporziano (Rome, Italy), 100 m from the shoreline. The climate is typically Mediterranean, with a pronounced summer drought and rain events concentrated in autumn and

spring. Mean monthly temperatures range between a minimum of 4–6°C and a maximum of 25–27°C. The proximity of the sea determines a high air humidity (rarely below 50%) that often leads to the formation of dew at night (Pitacco et al., 1992). The soil is a regosol with some organic matter in the first horizon, which is also rich in fine roots. The vegetation of the studied site is composed of patches of Mediterranean maquis and garigue. The latter are *Helichryso stoechadis-Cistetum eriocephali* or *Erico-Rosmarinetum*, characterized by the abundant presence of *Rosmarinus officinalis* and *Erica multiflora*; *Arbutus unedo* and *Phillyrea latifolia* are frequent species (Pignatti, 2001). The site is dominated by *Q. ilex*, with a maximum height of 3 m. For a detailed description of site characteristics and vegetation composition and distribution, see Fares et al. (2009).

2.2 Environmental monitoring

A net radiometer (Kipp & Zonen, NL) a Photosynthetic Active Radiation (PAR) meter (190 SZ, Licor, Lincoln, NE, USA) and a barometer (PTB101B, Vaisala, FI) were placed at 2 m above the canopy, while three thermo-hygrometer probes (50Y, Campbell, USA) were placed at 0.1, 1, and 3.5 m height, respectively, on an aluminum scaffold. The VPD (kPa) was calculated based on air temperature (T_a, °C) and relative humidity (RH, %) by using Murray's formula (Murray et al., 1967).

SWC (% v/v) was measured at four different depths (10, 40, 80, and 100 cm) in three different positions (bare soil, covered soil, partially covered soil) with three Time Domain Reflectometer (TDR) probes (soil profiler PR2, DeltaT Devices, UK). Minimum and maximum water contents, measured by the TDR were against gravimetrical mesurments. On 27 May and on 4 August the water table depth and the maximum rooting depth were determined by excavating two pits 1 m×2 m. In these days also the SWC at 150 cm depth and 10 cm above the water table was measured with a TDR probe horizontally inserted in the soil for 30 min. After this period soil samples were extracted and their weight measured immediately. When necessary, the SWC at 150 cm depth was extrapolated by fitting an exponential equation to the SWC measured by the TDR probes at the four different depths and the SWC 10 cm above the water table.

All sensors were connected to a CR10 data logger (Campbell, USA) which acquired data every minute and stored them as 30 min averages.

2.3 Stand structure and structural changes

Plant Leaf Area (LA, m^2) to Sapwood Area (SA, m^{-2}) ratio (LA/SA, x 10^{-2} m^2 m^{-2}) was measured in May and July following the protocol described in Fares et al. (2009). Leaf Mass per Area (LMA, g cm^{-2}) was derived by using the same values of leaf area (cm^2) and leaf mass (g) used to determine leaf biomass in Fares et al. (2009).

2.4 Leaf level measurements

Leaf-level gas exchange and water potential measurements were performed on *A. unedo*, *Q. ilex* and *P. latifolia*. Gas exchanges and microclimatic data were measured during spring and summer 2007, on six different days (25 May; 11, 15, and 27 June; 5 and 21 July) in the morning (08:00–09:00 and 10:00–11:00 GMT+1), at midday (12:00–14:00 GMT+1) and in the afternoon (16:00–17:00 GMT+1) on sun-exposed, fully developed leaves. Net photosynthesis (An, μmol CO_2 m^{-2} s^{-1}), leaf transpiration (E_l, mmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mmol H_2O m^{-2} s^{-1}) and sub-stomatal CO_2 concentration (C_i, ppm) were measured simultaneously by a portable open-system CIRAS I (PP Systems, Hitchin, UK). Environmental parameters such as irradiance (PAR, μmol photons m^{-2} s^{-1}), relative humidity (RH, %), T_a and leaf temperature (T_{leaf}, °C) were also recorded by the instrument; Vapour Pressure Difference between leaf and air was then calculated (VPD_l, mbar). For each measuring day, 27 to 45 leaf measurements were carried out on 3 to 5 representative adult trees for each species.

Midday leaf water potential ($\Psi_{l,MD}$, MPa) was measured with a Scholander chamber (PMS Instruments, Oregon, USA) during four different days (15 and 27 June; 5 and 21 July). A minimum of four leaves per species, coming from different individuals, was sampled immediately after the gas exchange measurements (12 to 20 measures on 4 to 5 individuals per species per day).

2.5 Sap flow measurements

Sap flow measurements based on the Heat Field Deformation system (HFD) (Čermák et al., 2004; Nadezhdina et al., 2004) were performed on four stems of *A. unedo* and *Q. ilex* from 15 May 2007 to 31 July 2007. Sap flow was measured with both radial and single point sensors on the same plants used for leaf level gas exchange measurments. Radial profile sensors were inserted in two stems per species with a diameter above 6 cm, allowing to measure sap flow at different depths, i.e. every 12 mm. Single point sensors were placed at 0.5 mm below cambium in stems with a diameter smaller than 5 cm. In all plants, sap flow was observable at all depths. The stem flow for the bigger stems was derived by integrating flows at different depth of each radial sap flow sensor, obtaining flows per section. The sapflow density in the tree was derived as average flow per section in agreement with the methodologies described in Čermák and Nadezhdina (1998) and Čermák et al. (2004). For the smaller stems flow was assumed to be uniform at all sapwood depths.

From the sap flow density of each tree, the species mean flow per unit leaf area (Q_l, mmol m^{-2} s^{-1}) was derived by dividing it by the mean LA/SA ratio.

All sap flow sensors were connected to a DL2 data logger (Delta-T devices, UK) which acquired data every minute and stored them as 10 min averages. DL2 and CR10 dataloggers were synchronized.

2.6 Canopy stomatal conductance and whole plant hydraulic conductance

Assuming that sap flow density scaled by the sapwood to leaf area ratio (Q_l, mmol m^{-2} s^{-1}) is equal to transpiration per unit leaf area, canopy stomatal conductance, (G_s, mmol m^{-2} s^{-1}) can be derived from sap flow measurements, based on a simplification of the Penman-Monteith equation (Whitehead and Jarvis, 1981; Pataki et al., 1998; Martínez-Vilalta et al., 2003):

$$G_s = \frac{\gamma \times \lambda \times Q_l}{\rho \times cp \times \mathrm{VPD}} \quad (3)$$

where γ is the psychrometric constant (kPa K^{-1}), λ is the latent heat of vaporization of water (J kg^{-1}), ρ is the density of air (kg m^{-3}), cp is the specific heat of air at constant pressure (J kg^{-1} K^{-1}) and VPD is the vapour pressure deficit (kPa), measured at canopy height. The VPD used for G_s derivation was the VPD at 1 m height. The simplification of the Penman-Monteith equation can be considered valid if G_s is considerably lower than the boundary layer conductance, G_b (Whitehead and Jarvis, 1981) i.e. when the canopy is strongly coupled with the atmosphere. The Mediterranean vegetation is known to be well coupled to the atmosphere also because of its small leaf size (Martínez-Vilalta et al., 2003). G_b was evaluated using the equation proposed by Jones (1992):

$$G_b = 6.62 \times \left(\frac{u}{d}\right)^{0.5} \quad (4)$$

where d is the average leaf size and u is the wind speed. G_b/G_s was always greater than 0.95.

For *A. unedo* and *Q. ilex*, leaf specific whole plant hydraulic conductance, K_p was evaluated by:

$$K_p = \frac{Q_{l,\max}}{\Psi_s - \Psi_{l,\mathrm{MD}}} \quad (5)$$

where $Q_{l,\max}$ (mmol m^{-2} s^{-1}) is sap flow per unit leaf area during peak transpiration at midday, $\Psi_{l,\mathrm{MD}}$ is leaf water potential ad midday and Ψ_s is the soil water potential (MPa) at 150 cm depth. The latter was derived from SWC through a soil water retention curve (pF curve) which describes the relationship between the logarithmic value of the soil water potential, Ψ_s, and the volumetric SWC (Schofield, 1935). The pF curve was obtained in laboratory using three soil samples. For *P. latifolia* instead, K_p could not be estimated from sap flow measurements because the stem diameter was too small (<3 cm). For this species, leaf level transpiration at midday ($E_{l,\mathrm{MD}}$), i.e. the 95 percentile of 15–20 measurements taken between noon and 14:00 UTC+1, was used instead of $Q_{l,\max}$ in Eq. 5 (cf., Magnani et al., 2002). In this case K_l is used to denote leaf specific whole plant hydraulic conductance. In order to better compare the changes in conductivity with those of the other two species the same computation is also reported for *A. unedo* and *Q.ilex*.

2.7 Statistical analysis

Statistical analyses were made with Statistica 7 software package (StatSoft, Inc. – Tulsa, OK – USA). Leaf data were analyzed by using a two-way Analysis of Variance (ANOVA) for repeated measurements taking into consideration species and date of measurements as explanatory factors (three levels for the first factor and four levels for the second), followed by the Newman-Keuls test at $p<0.05$. Data were previously tested for normality by using the Levene test at the significance level of 0.05. Data in figures and tables are presented as mean value ± standard deviation.

3 Results

3.1 Environmental monitoring

Cloudy or partially cloudy days were rare during the measuring period allowing for a fairly constant net radiation (data not shown). Air temperature increased during the season with mean daily values ranging between 18.3 and 24.8°C (Fig. 1a). Mean daily RH remained in the range 60–80% throughout the campaign, while VPD increased as a consequence of the increase in temperature (Fig. 1a).

At the beginning of the experimental period, SWC (Fig. 1b) was as low as 3% in the first 10 cm, rich in fine roots. However, this low value should be taken with caution because soil disrupture is likely to have occurred at this depth during probe insertion, and also because the organic matter at this depth clearly shrunk as the soil dried, creating open spaces between the soil and the probe. The few mm of rain fallen on 29, 30, and 31 May influenced only the top soil layer for a limited time period. Both at 40 and 80 cm, water content dropped to 5.8% on 30 May, while it declined less rapidly at 100 cm, reaching a constant value of ∼5.8% from the beginning of July. Figure 1b also shows the SWC values measured at 150 cm depth on the 27 May, and those extrapolated for other four days. Ψ_s estimated from the pF curve (Fig. A1) in the first 80 cm of soil was rarely above −3 MPa (data not shown). The Ψ_s at 150 cm depth, which was found to be the maximum rooting depth, varied between −1.5 MPa and −1.8 MPa (Fig. 2).

3.2 Stand structure and structural changes

Table 1 shows structural parameters of the three studied species, obtained with the procedure described in Fares et al. (2009). It is worth noting that all species developed new leaves during mid May, but while *Q. ilex* and *P. latifolia* showed no significant alteration in the LA/SA ratio, *A. unedo*

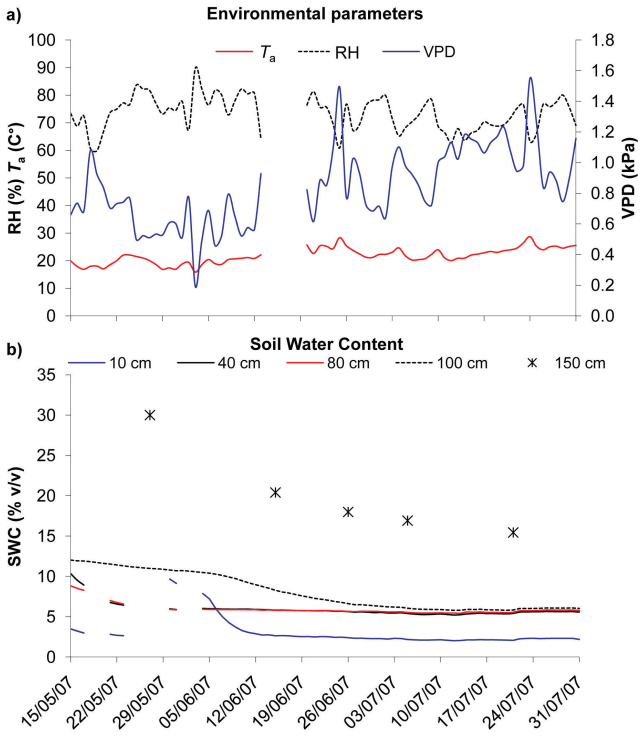

Fig. 1. Trend of environmental parameters, measured from 15 May 2007 to 31 July, 2007. **(a)** Air temperature (T_a, °C), Relative air Humidity (RH, %) and Vapour Pressure Difference (VPD, kPa), at canopy height; b) Soil Water Content (SWC, % v/v) at 10 cm, 40 cm, 80 cm, 100 cm, and 150 cm. Values at 10 cm, 40 cm, 80 cm, and 100 cm are daily means of three TDR probes, placed in different positions (bare soil, covered soil, partially covered soil); values at 150 were measured on 27 May and on 4 August, and extrapolated for the other dates as described in the text. Missing data are due to data logging interruption.

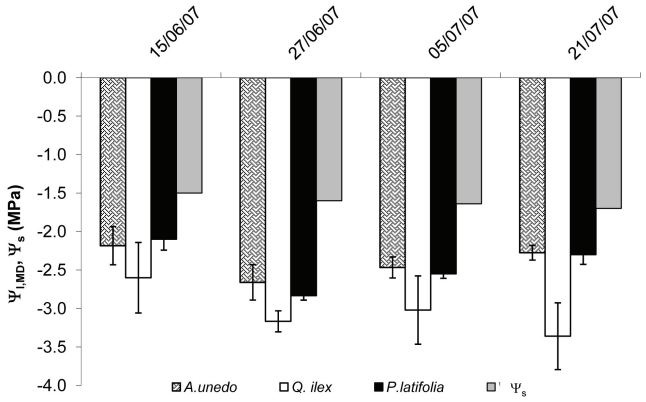

Fig. 2. Midday leaf water potential ($\Psi_{l,MD}$, MPa), measured in four sampling dates on *A. unedo*, *Q. ilex* and *P. latifolia* (means ± standard deviations, 4 to 5 measurments on 4 to 5 individuals, $4 \leq N \leq 5$), and Soil Water Potential at 150 cm (Ψ_s, MPa) as a proxy of predawn leaf water potential, extrapolated from the SWC values of Fig. 1.

Table 1. Structural parameters of *A. unedo*, *Q. ilex* and *P. latifolia*, obtained as described in Fares et al. (2009). Leaf area to Sapwood Area (LA/SA, $m^2\ m^{-2}$) was measured in May and July, while Leaf Mass per Area (LMA, $g\ cm^{-2}$) was measured only in May.

Parameters	*A. unedo*	*Q. ilex*	*P. latifolia*
LA/SA, May (x 10^{-2} $m^2\ m^{-2}$)	23.9±1.2	21.9±1.8	15.7±2.0
LA/SA, July (x 10^{-2} $m^2\ m^{-2}$)	15.2±1.5	24.0±1.3	16.4±1.8
LMA, May ($g\ cm^{-2}$)	0.0168±0.003	0.0198±0.003	0.0236±0.005

reduced its value from 23.9±1.2 (May) to 15.2±1.5 (July). Leaf Mass per Area (LMA) was lowest in *A. unedo* and highest in *P. latifolia*.

3.3 Leaf level measurements

Both *A. unedo* and *P. latifolia* showed relatively constant $\Psi_{l,MD}$ values during the experimental period, with no significant difference between the two species in each measurement day (p=0.53, 0.41, 0.53, and 0.74, respectively). *Q. ilex* instead showed decreasing values of $\Psi_{l,MD}$ during the season which became significantly lower than the other two species in the last day of measurements (p=0.003 and p=0.003 with respect to *A. unedo* and *P. latifolia*, respectively) (Fig. 2).

Figure 3 highlights the different seasonal patterns of *An*, E_l and g_s of the three studied species. *A. unedo* had the highest stomatal conductance at the end of May (p=0.00004), with daily mean values as high as 170.5±71.0 mmol $H_2O\ m^{-2}\ s^{-1}$ (Fig. 3c). Concomitantly with the decrease of SWC at 100 cm, the gas exchange rates of this species decreased gradually until the end of June (5.5±2.8 μmol $CO_2\ m^{-2}\ s^{-1}$ and 61.7±34 mmol $H_2O\ m^{-2}\ s^{-1}$ for *An* and g_s, respectively), and remained constant therafter (Fig. 3).

Q. ilex maintained fairly constant gas exchange rates during the whole campaign, although a slight reduction of g_s, not statistically significant (p=0.06), occurred on 21 July (45.5±30.0 mmol $H_2O\ m^{-2}\ s^{-1}$) (Fig. 3c).

As for *P. latifolia*, it showed the highest, statistically significant values of g_s and *An* in mid June (159.2±29.0 mmol $H_2O\ m^{-2}\ s^{-1}$ and 11.6±1.5 μmol $CO_2\ m^{-2}\ ^{-1}$, respectively), followed by a 33% reduction in g_s and 12% in *An*; despite this reduction, *P. latifolia* maintained the highest gas exchange rates at the end of the experimental period (21 July 2007) compared to the other two species (Fig. 3a–c).

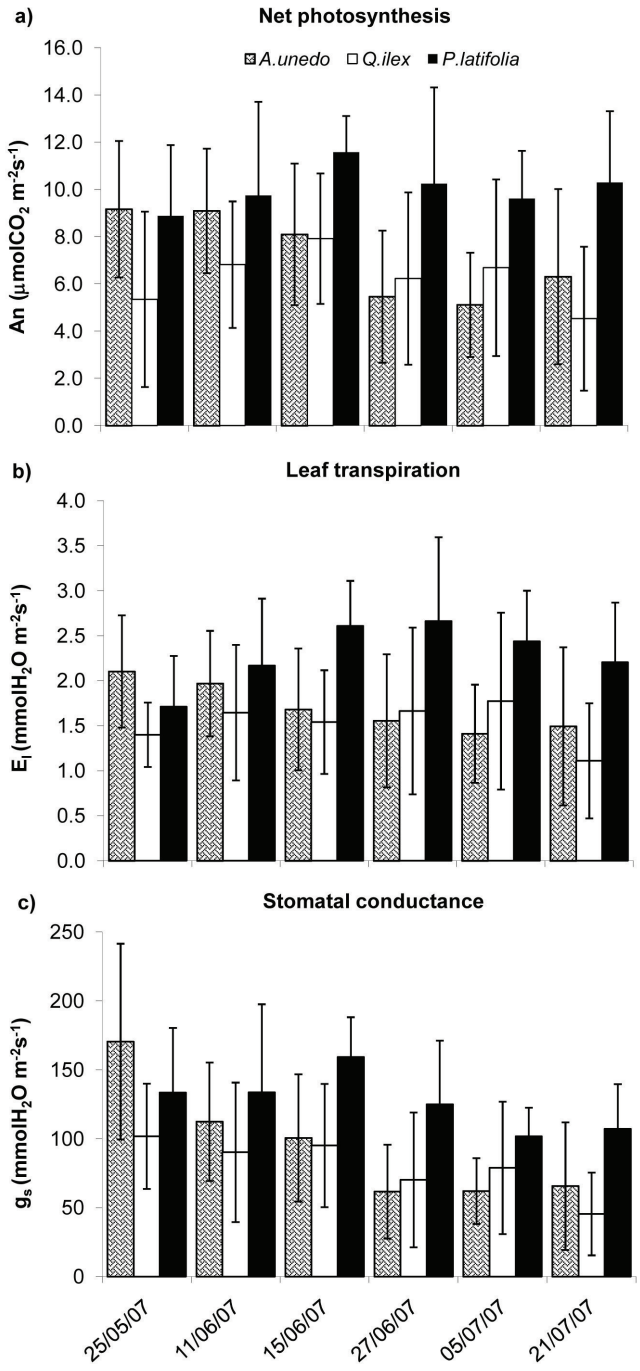

Fig. 3. Daily average of net photosynthesis (An, μmol CO_2 m^{-2} s^{-1}) **(a)**, stomatal conductance (g_s, mmol H_2O m^{-2} s^{-1}) **(b)**, and leaf transpiration (E_l, mmol H_2O m^{-2} s^{-1}) **(c)**, measured on *A. unedo*, *Q. ilex*, and *P. latifolia*. Data are means ± standard deviations, $27 \leq N \leq 45$.

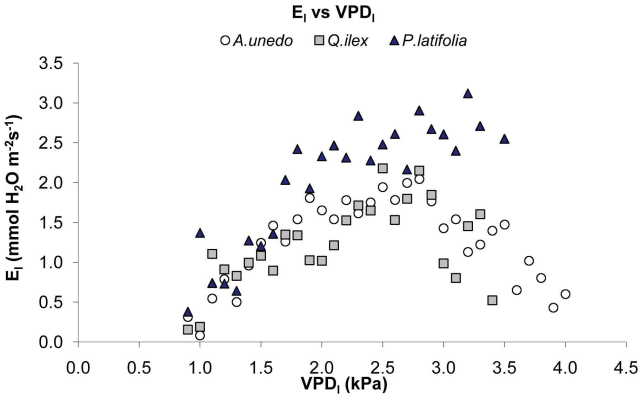

Fig. 4. Relationship between mean Vapour Pressure Difference based on leaf temperature (VPD_l, kPa) and mean leaf transpiration (E_l, mmol H_2O m^{-2} s^{-1}) for *A. unedo*, *Q. ilex*, and *P. latifolia*. $27 \leq N \leq 45$.

The relationship between vapour pressure difference based on leaf temperature, VPD_l, and E_l, was bell shaped for both *Q. ilex* and *A. unedo*, reaching a maximum value at 2.6 kPa; E_l of *P. latifolia* instead raised continuously, but with a decreasing slope for VPD>2.8 kPa. (Fig. 4).

3.4 Sap flow, canopy stomatal conductance and whole plant hydraulic conductance

Figure 5a and b shows the sap flow of the three species during the experiment. Between mid May and the end of July, both *A. unedo* and *Q. ilex* showed a decline in $Q_{l,\max}$ concomitant with the reduced SWC (Fig. 6) and the higher evaporative demand. As observed from leaf level gas exchanges, $Q_{l,\max}$ of *A. unedo* decreased a 41% linearly with the SWC at 100 cm, until the end of June (R^2=0.88). However, unlike observed at leaf level, $Q_{l,\max}$ continued to decrease (13%) even when the SWC at 100 cm remained constant at a value of ∼5.8%. In *Q. ilex* instead, $Q_{l,\max}$ slightly decreased (15%) in the same SWC range (R^2=0.25), after which it declined by only another 6%. For this reason, given the constant SWC, it is not possible to correlate $Q_{l,\max}$ with SWC for both species after the end of June (Fig. 6).

G_s, estimated from sap flow measurements (Eq. 3) at saturating light intensities (PAR>1000), declined as the VPD increased following a logarithmic curve in both *A. unedo* and *Q. ilex* (Fig. 7a and b). While in *A. unedo* the relationship changed considerably before and after 20 June, with a slope reduction of 55.5%, the same relationship changed only slightly in *Q. ilex*, whose slope was reduced by 37.0%; this suggested a higher loss of K_p in *A. unedo* than in *Q. ilex*.

The species-related differences in losses of K_p are confirmed by the K_p values estimated as in Eq. (5). In the course of the dry season, *Q. ilex* showed a small reduction in K_p (from 0.69±0.11 to 0.42±0.07 mmol H_2O m^{-2} s^{-1} MPa^{-1}) as compared to the loss in *A. unedo* (from 1.78±0.29 to

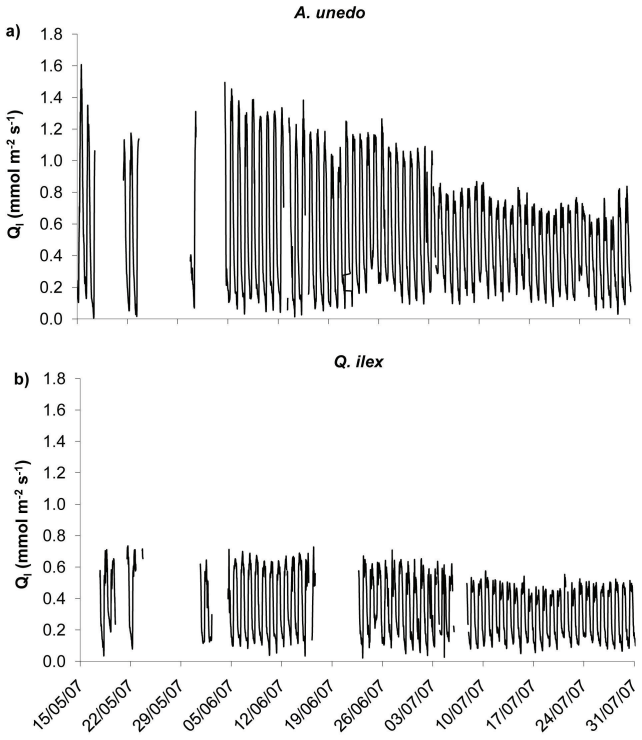

Fig. 5. Seasonal trend of sap flow (Q_l, mmol H_2O m^{-2} s^{-1}) of *A. unedo* **(a)** and *Q. ilex* **(b)**, measured from 15 May 2007 to 31 July 2007. Missing data are due to data logging interruption.

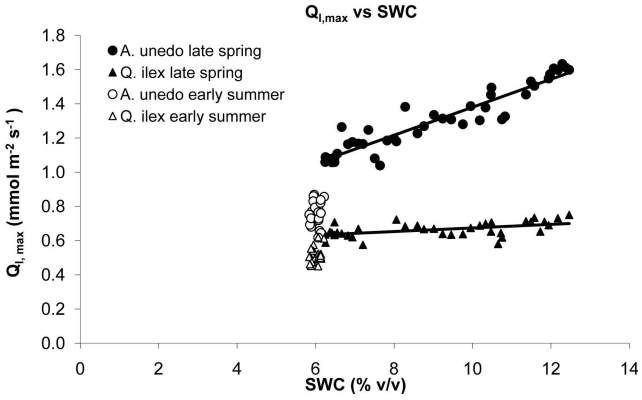

Fig. 6. Relationship between Soil Water Content (SWC, % v/v) and daily maximum Sap flow ($Q_{l,\max}$, mmol m^{-2} s^{-1}) for *A. unedo* and *Q. ilex*. Closed symbols: before 20 June; open symbols: after 20 June.

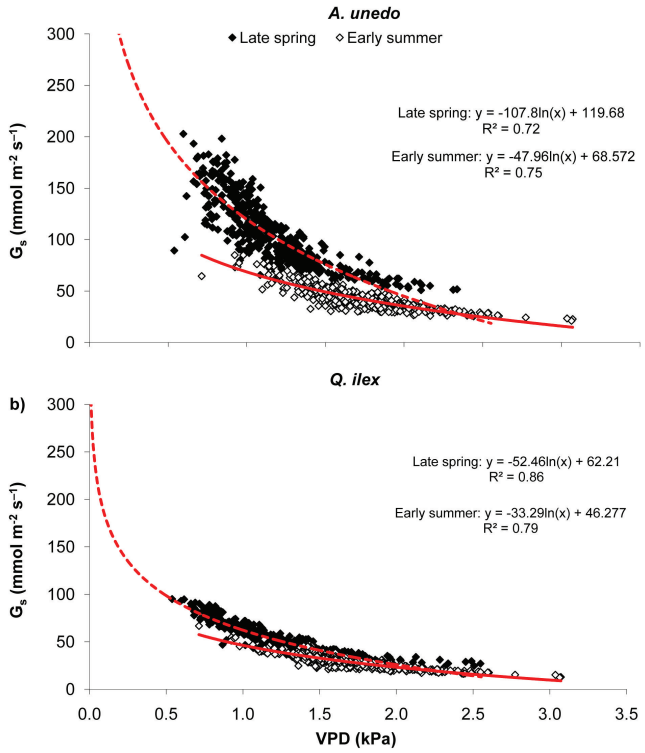

Fig. 7. Relationship between canopy stomatal conductance (G_s, mmol m^{-2} s^{-1}), estimated from Sap flow measurements at saturating light intensities (PAR>1000), and Vapour Pressure Difference (VPD, kPa), measured at canopy level for *A. unedo* **(a)** and *Q. ilex* **(b)**. Closed symbols: before 20 June; open symbols: after 20 June. The slope reduction between the two period is 55.5% and 37.0% for *A. unedo* and *Q. ilex*, respectively.

0.74±0.12 mmol H_20 m^{-2} s^{-1} MPa^{-1}) (Fig. 8a). Figure 8b also shows an increase of K_l in *P. latifolia* during the season from 2.47±0.54 to 3.97±0.18 mmol H_2O m^{-2} s^{-1} MPa^{-1}. It is worth noting that for both *A. unedo* and *Q. ilex* K_p and K_l showed the same trend, even if values are not comparable due to upscaling reasons: K_p integrates the transpiration rate of all leaves considered together independently from their immediate surrounding environment where light is the variable that changes the most, K_l instead refers uniquely to sunlit leaves which are not necessarily representative of the whole canopy.

The radial sap flow sensors allowed to measure sap flow at different depths from the cambium, and hence to highlight changes in the radial pattern of sap flow. Changes in the radial pattern of sap flow were strong for *A. unedo* where flow was nearly evenly distributed throughout the xylem in the beginning of the season but, as the season progressed, a larger percentage of the total flow occurred in the deeper xylem (Fig. 9a). In *Q. ilex* instead, the radial pattern did not change during the season (Fig. 9b).

4 Discussion

In the Castelporziano Estate, the year 2007 was very warm, with high levels of drought stress index also in winter months (Fares et al., 2009), monthly precipitation never exceeding 100 mm, and total yearly rainfall (480 mm) lower than the historical mean of 740 mm (Manes et al., 1997b).

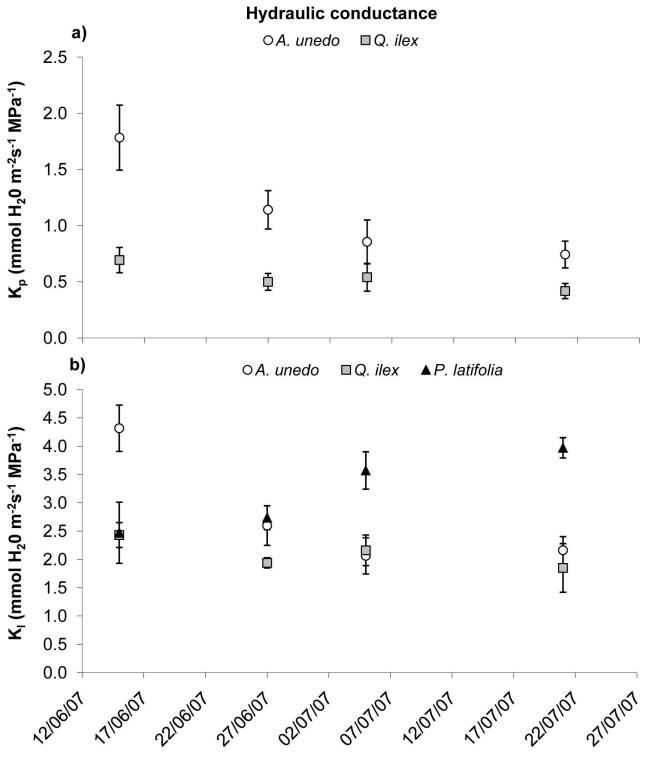

Fig. 8. Leaf specific whole plant hydraulic conductance, calculated from sap flow measurements for *A. unedo* and *Q. ilex* (K_p, mmol H_2O m^{-2} s^{-1} MPa^{-1}) **(a)**, and from leaf level transpiration measurements also for *P. latifolia* (K_l, mmol H_2O m^{-2} s^{-1} MPa^{-1}) **(b)**. In order to better compare the changes in conductivity of this latter species with those of the other two species, the same computation is also reported for *A. unedo* and *Q. ilex*. Values of K_p and K_l are not quantitatively comparable because of upscaling reasons, as explained in the text.

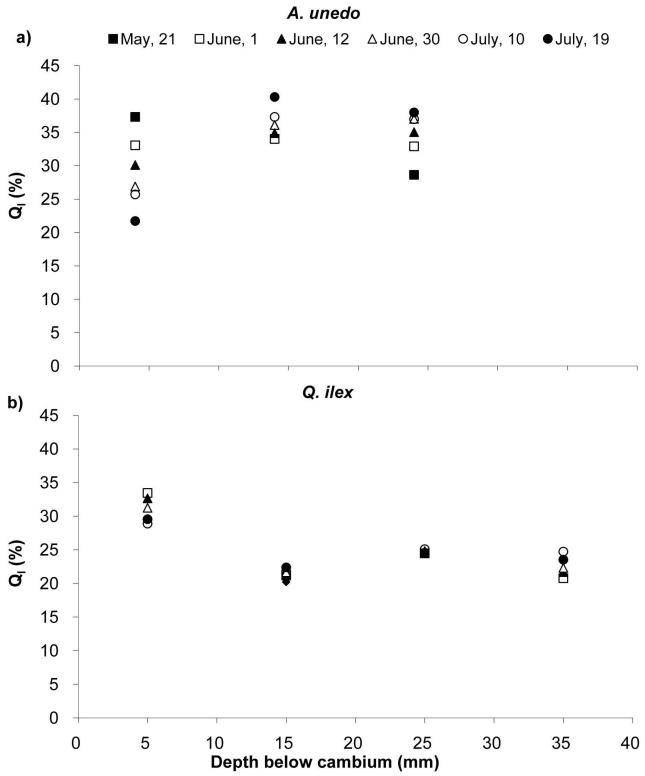

Fig. 9. Changes in the radial profile of *A. unedo* **(a)** and *Q. ilex* **(b)** during the experimental period. Data points indicate the percentage contribution of each depth to the total stem flow. Each value represents the mean of two stem per species, which were chosen with similar diameter: 32–35 mm for *A. unedo* individuals, and 39–43 mm for *Q. ilex* individuals.

As expected, the response to drought involved both the physiology and the plant structure. The physiological response to the increasing drought stress in the period from spring to high summer, was species-specific as observed earlier by Martínez-Vilalta et al. (2003), Ogaya and Peñuelas (2003) and Gratani and Varone (2004). Seasonal trend of the physiological parameters was similar to that found by other authors, both for sap flow in a Spanish site (Martínez-Vilalta et al., 2003), for leaf level measurements recorded in Tuscany (Tognetti et al., 2000b) and in a nearby site inside the Presidential Estate of Castelporziano (Gratani and Bombelli, 1999). Our LA/SA values, instead, compared with those reported by Martínez-Vilalta et al. (2003), were similar only for *Q. ilex* (24.0±1.3 vs. 24.2±4.2) and considerably higher both for *A. unedo* (15.2±1.5 vs. 9.5±0.5) and *P. latifolia* (16.4±1.8 vs. 8.8±0.3). Such a strong difference is unlikely due to the different methodologies used to assess LA/SA (tree-level estimates vs branch level estimates in Martínez-Vilalta et al., 2003). Instead, as found for other species by other authors, it is likely that *A. unedo* and *P. latifolia* respond to the higher evaporative demand and aridity of the Spanish site by reducing the LA/SA ratio which implies a raise of available water per unit leaf area (Eq. 2). The conservative LA/SA value of *Q. ilex* suggests that this species not only maintains an unaltered LA/SA value in different light environments, as reported by Sanchez-Vilas et al. (2007), but also in environments with contrasting water availability.

Despite the similar sap flow trend, the comparison with the results of Martínez-Vilalta et al. (2003) highlights different relative responses for the three species. In our case *A. unedo*, and not *Q. ilex*, was subject to the highest reduction in Q_l (Fig. 5). Our results also differ in terms of $\Psi_{l,\mathrm{MD}}$ which was lower at the Spanish site; additionally, at the Spanish site, $\Psi_{l,\mathrm{MD}}$ was clearly proportional to the predawn Ψ_l, while our $\Psi_{l,\mathrm{MD}}$, despite the absence of rainfall, did not vary from 15 June to the end of July, with the exception of the slight decrease observed for *Q. ilex*. These differences are clearly due to the presence of a relatively shallow water table at the Castelporziano site (Busuoli et al., 2001). Accordingly, the values and trend of $\Psi_{l,\mathrm{MD}}$ measured at our site for *Q. ilex* are comparable to those reported by Bussotti et al. (2002) in a Tuscan site, where the vegetation response to the driest period was also influenced by the groundwater level.

The presence of a water table does not allow to clearly discriminate which water use strategy (isohydric or anisohydric, sensu Tardieu and Simonneau, 1998) these species adopt. In fact, if roots have unlimited access to groundwater, the water use by the species should not be limited by rainfall. In absence of groundwater instead, a stronger water stress is usually observed (Bussotti et al., 2002). In our case the response can be considered moderate: $\Psi_{l,\mathrm{MD}}$ values of *A. unedo* and *P. latifolia* were well inside the critical tension for embolism known for these species (Martínez-Vilalta et al., 2002; Corcuera et al., 2004), while the values observed for *Q. ilex* may be the cause for a moderate embolism. All values are those usually reported for Mediterranean species during drought stress (Manes et al., 2006; Tognetti et al., 2000b; Serrano et al., 2005). Nevertheless, stomatal control and reduction of sap flow took place concomitantly with a sharp decline in SWC in the upper soil layers. This reduction is particularly evident for *A. unedo*, where $Q_{l,\max}$ (Fig. 6) and the slope of the G_s vs. VPD plot (Fig. 7) were affected by the decline in SWC after 20 June.

At any given value of VPD, transpiration decreases with decreasing SWC, implying a higher stomatal sensitivity to available water rather than to leaf water potential. Given the presence of a relatively shallow water table, the different drought response of the three species may be explained by a different below-ground root distribution (Bréda et al., 2006). It is common for Mediterranean species to rely both on occasional rain-fed SWC in the superficial soil layers and on water resources stored in the deeper soil layers (Tognetti et al., 2009) and the water use may differ depending on the resource. The presence of a water table and the sandy nature of the soil, which is subject to rapid changes in its SWC, represents an extreme case of this differential water resource use. Moreover, in these environmental conditions it becomes more complicated to discuss water availability in terms of Ψ_s at a determined depth when it is used as a proxy of extractable water (Lundblad and Lindroth, 2002).

Plants with prevalently superficial roots are to suffer drought during summer, while plants with a dependence on a reliable water resource are likely to respond weakly to summer drought (Castillo et al., 2002). A third situation is represented by plants with roots distributed between the superficial layers and the water table: these may show a dual behaviour, as the changes in vertical distribution of the water resource will be reflected in a change of absorbing surface. The observed sap flow radial pattern profiles (Fig. 9) suggest that *A. unedo* and *Q. ilex* have a different distribution of the root absorbing surfaces. In fact, according to Nadezhdina et al. (2008), superficial roots are mainly connected with the outer xylem, while the deep roots are preferentially connected with the inner xylem. The observed change in radial pattern in *A. unedo*, but not in *Q. ilex*, thus suggests that *A. unedo* should have more evenly vertically distributed roots, being able to use both water resources (superficial water, when present, and groundwater), while *Q. ilex* should draw most water from a reliable water resource (water table). The different distribution of the absorbing root surface and the different use of water resources by the studied species in this site is confirmed by Alessio et al. (2004). Using oxygen isotope ratios, these authors were able to determine the provenance of water used by *A. unedo*, *Q. ilex*, and *P. latifolia*: superficial (typically coming from late spring-summer precipitation) or groundwater (accumulated during the abundant autumn-winter and early spring precipitation). Their results clearly show that while *Q. ilex* and *P. latifolia* both draw most of the water from the water table, *A. unedo* uses both superficial and deep waters, i.e. the roots of *Q. ilex* and *P. latifolia* are mostly distributed in the deeper layers, while the roots of *A. unedo* are more evenly distributed between the top and deep soil layers. We argue that the loss of hydraulic conductance of the species reflects their relative change from a dual water resource to the sole water table resource. From Alessio et al. (2004) it is also deductible that *P. latifolia* is the species that draws water almost exclusively from the deeper water resources, i.e. the species with the deepest rooting system.

Because of the different root distribution *A. unedo* undergoes the largest loss of K_p during drought, while *Q. ilex* only shows a minor loss and a *P. latifolia* has no loss (Figs. 7 and 8). This different loss of K_p determines a strong dependency of the primary productivity of *A. unedo* on rainfall. Noticeably, *P. latifolia* increased K_l, an increase that cannot be explained solely by a negligible loss in root absorbing surface, and possibly implies an increased root permeability.

Plants may strongly modify root permeability by rapid changes in the density of aquaporins in cell membranes (Kaldenhoff et al., 2008). A loss in root surface (lower K_p), could hence be compensated with an increase in permeability (higher K_p), of the remaining roots. Changes in permeability may also compensate for reduced water availability, allowing to some extent to keep Ψ_l constant independently from SWC. This mechanism has been reported for a *Vitis* hybrid (Galmés et al., 2007) and allowed for an adequate water supply even at low SWC.

Recalling Eq. (2) to summarize the different coordination mechanisms of the species, it emerges that *A. unedo* is the species that responds most drastically to environmental changes and it does so by modifying both physiological and structural parameters: a reduction in transpiration by strong stomatal control and a reduction of the LA/SA ratio in order to keep Ψ_l under the critical value for embolism. This ability allows *A. unedo* to efficiently exploit occasional rain fed superficial waters, and to rely on water resources stored in the deeper soil layers to overcome summertime aridity. *Q. ilex* instead is the only species that compensates for the decrease of water availability in the upper soil layers by lowering its $\Psi_{l,\mathrm{MD}}$, allowing to keep transpiration almost constant during the course of the season. The decline in G_s of *Q. ilex*, observed during the experimental period, can be attributed only minimally to the decrease in SWC in the shallow soil layers, contrary to what was observed for *A. unedo*.

Finally, *P. latifolia* not only compensates for the loss in root surface by increasing root permeability, but increases K_l in order to allow for a high g_s even when the transpirative demand increases, a response which is in agreement with its known drought tolerance (Serrano and Peñuelas, 2005).

5 Conclusions

Coastal dune ecosystems are often characterized by strong time and space variability of water resources, an environmental characteristic to which species may adapt differently. In this complex environment, it appears that water use strategies of the maquis species cannot be described solely in the frame of the isohydric/anisohydric behavior. An integrated approach, combing leaf level, whole plant level and structural measurements, allowed to highlight more complex mechanisms and that the relative competitive ability of the three species requires a deeper knowledge of how different plant compartments coordinate. Additionally, the adaptation to site-specific environments may bring to an inversion of the ranking of species in terms of responses to drought, as shown by the comparison with previous studies (e.g. Martínez-Vilalta et al., 2003). Moreover, it is interesting to notice that the species with the most constant transpiration (*Q. ilex*) is also the one that maintains an unaltered LA/SA both during the season and when compared with other sites (Manes et al., 1997c), while the other two species, known to be mid-successional species, present more variability in transpiration and in structure in response to environmental conditions (Castro-Díez and Montserrat-Martí, 1998). In particular, we found that, for *A. unedo*, the rapid adaptation to environmental variability implies both physiological and structural adjustments, making it highly competitive in the Mediterranean plant community (Vitale and Manes, 2005). However, since *A. unedo* showed the highest assimilation rates only when a sufficient amount of superficial water was still available (i.e. spring), our results, although restricted to a short period of observation, suggest that in sites with a dual water resource, modified rainfall patterns under future climate should be also considered. It can be argued that, if the prolonged drought period foreseen by Regional Circulation Models for the Mediterranean Basin (IPCC, 2007) will affect spring months, the competitive performance of *A. unedo* may be strongly reduced, thus affecting the dynamism of the Mediterranean maquis phytocenosis. In general the relative competitive ability of the three species depends on the length of the period during which water in the upper soil layers remains extractable.

In the frame of the ACCENT-VOCBAS field campaign, the present work has contributed to a better understanding of the complexity of environmental, physiological and structural factors influencing the behaviour of sandy dune plants, particularly in terms of gas exchanges through stomata. This is particularly important for the quantification of the interactions between Mediterranean vegetation and the atmosphere, in terms of BVOC emissions, pollutant and carbon uptake. Our results highlight that physiological and structural adaptation to site-specific environmental conditions should be taken into account when investigating the plant-atmosphere interactions under Mediterranean climatic conditions.

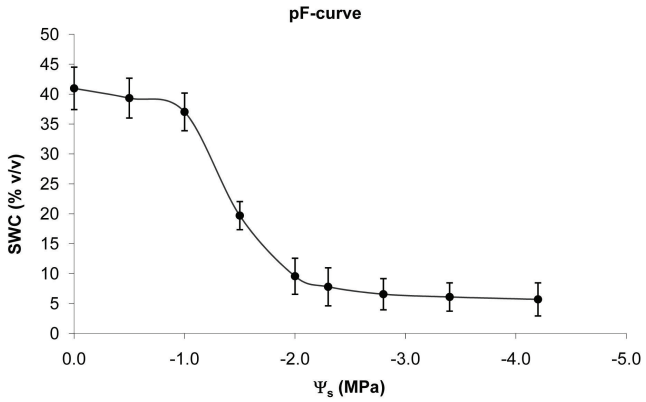

Fig. A1. pF curve, derived in laboratory condition according to Schofield (1935), describing the relationship between the value of the soil water potential, Ψ_s (MPa) and the volumetric SWC (% v/v). Data reported are mean ± standard deviation of 3 soil samples.

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